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GENETIC RELATIONS OF THE WINGED AND
WINGLESS FORMS TO EACH OTHER AND
TO THE SEXES IN THE APHID MACRO-
SIPHUM SOLANIFOLII

DR. A. FRANKLIN SHULL

UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN

INTRODUCTION

LIFE cycles are known, in many aphid species, from field observations alone. A number of cycles have been determined from breeding experiments upon aphids in confinement. Often, however, these experiments appear not to have used the pedigree method. In the course of some work on the potato aphid, *Macrosiphum solanifolii*,¹ I observed indications of peculiarities in the genetic relations of the various forms to each other, which could be detected only by the pedigree method. Experiments designed to demonstrate these relations were instituted, with the results described in this paper.

Macrosiphum solanifolii, as observed in these experiments, comprises four kinds of individual: (1) the apterous viviparous female, which is green; (2) the alate viviparous female, which is also green; (3) the oviparous or sexual female, which is wingless and of a yellowish-green color until late in life, when the abdomen becomes filled with green eggs which impart a green color to the female herself; and (4) the male, which is winged and of a brown or brown and green color. Of these types of individual, the alate female can be recognized when a little more than half grown by her wing pads. The oviparous female has thickened brown hind tibiæ covered with sensoria, which are recognizable with the unaided eye, and which develop a few days before maturity. The male

¹ Identified by Dr. Edith M. Patch.

is usually, though not always, distinguishable at birth because of its pink or gray color, and those that are green at birth usually develop the gray or pink color within a few days. This color of the immature male has not, I believe, been recorded in the published descriptions of the species, and it is not impossible that it is a characteristic of certain parthenogenetic lines only.

Miss Patch (1915) has described a pink variety of each of the viviparous forms. I have never seen these in my experiments, though thousands of individuals have been examined, except in diseased animals which died shortly after discovery. The immature pink aphids in my experiments have all been males. The occurrence of pink females is probably a characteristic of certain parthenogenetic lines.

In my experiments the potato has been exclusively used as the host plant. These plants were reared in pots and were covered with lantern globes closed at the top with muslin.

EXPERIMENTS

Relation of Winged and Wingless Forms to Each Other

Experiment 293.—Starting with sister individuals, two lines were bred for three generations, one line from apterous parents exclusively, the other from alate parents only. As in the other experiments to be described, about a dozen adult females were placed together on a single plant, to become parents of the following generation. When they began to produce young, the latter were removed daily, or every two days, to young plants. Successive groups of young were placed on one plant until they seemed likely to become too crowded (usually not over 150 per plant), after which a new plant was used. As many as five plants were required in some cases to receive the young of one lot of parents. In the tables these plants are designated, in the columns headed "Host Plant," as first, second, third, etc. As the young aphids became adult they were removed and either used for further breeding or destroyed.

As a rule the parents for the following generation were taken from the first of the host plants, and were transferred to a young healthy plant, on which they produced their young.

This particular experiment was started in June from a stock whose stem mother hatched in the greenhouse in the preceding January. The line had passed through a sexual phase in that time, but had been preserved by a small number of viviparous females. In Table I the line from apterous parents is represented in the upper half of the table, the line from alate parents in the lower half. For the sake of comparison the totals are placed together at the bottom of the table.

TABLE I

CONTRASTING THE OFFSPRING OF APTEROUS PARENTS AND THOSE OF ALATE PARENTS IN THE APHID *Macrosiphum solanifolii*

Genera-tion	Parents	Host Plant	Dates of Isolating Young	Offspring				
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males	
I.....	Apterous	First	June 27-June 30	49	64	0	0	
		Second	July 2	35	73	0	0	
		Third	July 4-July 5	33	48	0	0	
		First	July 7-July 9	22	118	0	0	
		Second	July 11	44	88	0	0	
		Third	July 13	21	62	0	0	
II....	Apterous	Fourth	July 14-July 16	27	28	0	0	
		First	July 18-July 21	47	29	0	0	
		Second	July 23	7	7	0	0	
I.....	Alate	First	[June 28-July 2	110	21	0	0	
II....	Alate	Second	July 4-July 6	32	2	0	0	
		First	July 9-July 11	66	29	0	0	
		Second	July 13-July 14	99	50	0	0	
		Third	July 16-July 18	62	52	0	0	
		Fourth	July 21	41	12	0	0	
		Fifth	July 23	14	4	0	0	
III...	Alate	First	July 21	80	23	0	0	
		Second	July 23	35	6	0	0	
		Third	July 24-July 26	5	3	0	0	
Totals from apterous parents				285	517	0	0	
Totals from alate parents				544	202	0	0	

There is a striking preponderance of winged offspring in the families of wingless parents, and a preponderance of wingless offspring from winged parents.

Experiment 294.—This was a repetition of the preceding experiment, in part simultaneous with it but of shorter duration. The method of conducting the experiment was the same as in the preceding experiment. Table II gives the results.

TABLE II

CONTRASTING TWO RELATED LINES OF *Macrosiphum solanifolii*, ONE REARED FROM APTEROUS PARENTS, THE OTHER FROM ALATE PARENTS

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	July 7-July 9	22	118	0	0
		Second	July 11	44	88	0	0
		Third	July 13	21	62	0	0
		Fourth	July 14-July 16	27	28	0	0
		First	July 18-July 21	47	29	0	0
		Second	July 23	7	7	0	0
II.....	Apterous	First	July 7-July 9	98	58	0	0
		Second	July 11	93	67	0	0
		Third	July 13	62	18	0	0
		Fourth	July 14-July 16	66	46	0	0
		Fifth	July 18	17	3	0	0
		First	July 18	65	10	0	0
II.....	Alate	Second	July 21	179	29	0	0
		Third	July 23-July 24	22	4	0	0
		Totals from apterous parents		168	332	0	0
		Totals from alate parents		602	235	0	0

The conclusion is the same as from Table I. Apterous parents give birth more largely to alate offspring, alate parents more largely to apterous offspring.

Relation of Winged and Wingless Forms to the Sexes

Experiment 303.—Just before the sexual phase of the cycle began a line from winged parents was started from a line being reared from wingless parents. In so far as the two were bred simultaneously their progeny are recorded in Table III.

Of the sexual offspring, the wingless parents produced exclusively males, while the wingless parents gave birth to a very large majority of sexual females. It may be

TABLE III

CONTRASTING THE PROGENY OF ALATE PARENTS WITH THE PROGENY OF
APTEROUS PARENTS, WITH SPECIAL REFERENCE TO THE SEXUAL FORMS,
IN THE APHID *Macrosiphum solanifolii*

Genera- tion	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Vivipa- rous Females	Alate Vivipa- rous Females	Ovipa- rous (Sexual) Females	Males
I.....	Apterous	First	Sept. 7-Sept. 9	68	2	0	0
		Second	Sept. 11-Sept. 13	33	37	0	0
		Third	Sept. 15-Sept. 19	0	14	0	36
		Fourth	Sept. 21	0	0	0	11
II.....	Apterous	First	Sept. 21-Sept. 23	0	62	0	0
		Second	Sept. 25-Sept. 27	0	17	0	0
		Third	Sept. 29-Oct. 9	0	2	0	59
		Fourth	?	0	0	0	11
I.....	Alate	First	Sept. 17-Sept. 19	6	9	0	0
		Second	Sept. 21-Sept. 23	7	0	8	12
		Third	Sept. 25-Sept. 27	0	0	19	1
		Fourth	Sept. 29-Oct. 5	1	0	14	4
II.....	Alate	First	Sept. 27-Sept. 29	0	0	27	0
		Second	Oct. 1-Oct. 7	0	0	62	0
		Third	Oct. 9	0	0	4	0
		Totals from apterous parents.....		101	134	0	117
Totals from alate parents.....				14	9	134	17

also pointed out that the conclusion regarding the relation of the winged and wingless viviparous females to each other that was drawn from Tables I and II is confirmed in Table III.

Progressive Change in the Frequency of all the Forms in Successive Generations

Confirmation of the conclusions drawn from the preceding experiments is found in several lines which were designed to show the normal life cycle over a considerable period when each generation was derived from wingless parents. In addition, these lines show a progressive change in frequency of both the winged and wingless viviparous forms and of the sexes. Owing to this progressive change it was not possible to maintain uniform parentage, since in the late generations there were no apterous individuals from which to breed. The principal lines were obtained in the three following experiments.

Experiment 299.—This was a line reared from a wingless female obtained out of doors about August 10. It was reared in the laboratory. Table IV records this line.

TABLE IV

A PARTHENOGENETICALLY-PRODUCED LINE OF *Macrosiphum solanifolii*, PRODUCED IN THE MAIN BY WINGLESS PARENTS

Note (1) the gradual transition from wingless to winged viviparous females; (2) the transition from viviparous (parthenogenetic) reproduction to sexual reproduction; and (3) the fact that the males are produced mainly by wingless parents, the sexual females chiefly by winged parents. See Experiment 299.

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	Aug. 24-Aug. 25	50	0	0	0
		Second	Aug. 27-Aug. 28	51	0	0	0
		Third	Aug. 30-Sept. 3	29	0	0	0
		First	Sept. 1	93	0	0	0
		Second	Sept. 3	149	0	0	0
		Third	Sept. 5-Sept. 7	49	0	0	0
II....	Apterous	Fourth	Sept. 5-Sept. 15	0	2	0	37
		Fifth	Sept. 9-Sept. 15	58	42	0	7
		Sixth	Sept. 17	4	1	0	0
		First	Sept. 9-Sept. 11	57	17	0	0
		Second	Sept. 13-Sept. 17	9	13	0	7
		Third	Sept. 19	0	0	0	9
III...	Apterous	First	Sept. 17-Sept. 19	13	86	0	0
		Second	Sept. 21-Sept. 23	1	30	1	13
		Third	Sept. 25-Sept. 27	0	0	0	15
		Fourth	Sept. 29-Oct. 10	0	0	0	11
IV....	Apterous	First	Sept. 27	6	81	0	0
		Second	Sept. 29	0	34	0	0
		Third	Oct. 1-Oct. 3	0	2	14	44
		Fourth	Oct. 5-Oct. 7	0	0	2	39
		Fifth	Oct. 9-Oct. 16	0	0	0	25
		First	Oct. 7-Oct. 9	2	17	3	0
V....	Apterous	Second	Oct. 11-Oct. 16	0	1	11	21
		Third	Oct. 20-Oct. 27	0	0	0	12
		Alate	First	Oct. 16-Oct. 25	0	0	24
		Second	Oct. 30-Nov. 6	0	0	4	0
		First	Oct. 18-Oct. 30	0	5	11	3
		Second	Nov. 6	0	0	0	1
VI....	Alate ²	First	Oct. 18-Oct. 20	0	0	134	0
		Second	Oct. 23	0	0	101	0
		Third	Oct. 25-Oct. 27	0	0	44	0
		Fourth	Oct. 30-Nov. 6	0	0	18	0
		First	Nov. 1-Nov. 3	0	0	50	0
		Second	Nov. 6	0	0	10	0
VII ..	Apterous	Third	Nov. 10	0	0	3	0

² The alate parents in the seventh and eighth generations were offspring of apterous parents.

Experiment 298.—This line was derived from the same female as Experiment 299, but was reared in the greenhouse. See Table V.

TABLE V

A PARTHENOGENETICALLY PRODUCED LINE OF *Macrosiphum solanifolii*, PRODUCED CHIEFLY BY APTEROUS PARENTS.

The same transitions noted in Table IV are observable here on a smaller scale. See Experiment 298.

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	Aug. 13	7	0	0	0
II....	Apterous	First	Aug. 15-Aug. 17	100	5	0	0
III...	Apterous	First	Aug. 24-Aug. 27	15	0	0	0
		Second	Aug. 28-Aug. 30	65	2	0	0
		Third	Sept. 1-Sept. 5	64	4	0	0
IV...	Apterous	First	Sept. 7-Sept. 9	68	2	0	0
		Second	Sept. 11-Sept. 13	33	37	0	0
		Third	Sept. 15-Sept. 19	0	14	0	36
		Fourth	Sept. 21	0	0	0	11
V....	Apterous	First	Sept. 21-Sept. 23	0	62	0	0
		Second	Sept. 25-Sept. 27	0	17	0	0
		Third	Sept. 29-Oct. 9	0	2	0	59
		Fourth	?	0	0	0	11
V ...	Alate	First	Oct. 13-Oct. 20	0	0	14	0
		Second	Oct. 23	0	0	4	0

Experiment 270.—The stem mother of this line hatched from a fertilized egg that was laid in the greenhouse in November and hatched in January. In March and April the line passed through a sexual phase, but a small number of viviparous females were produced during this period and by them the parthenogenetic line was continued. The families were not fully recorded until the latter part of May. Table VI includes only the records beginning May 28. Nine generations are there recorded as if an uninterrupted line, but an explanation is necessary. In the midst of the fifth generation the aphids began to die in large numbers for an unknown reason. In a few days every aphid out of hundreds was dead. Fortunately two or three aphids were found on a discarded plant in the greenhouse. Since only this one line had been reared in the greenhouse up to that time I felt

TABLE VI

A PARTHENOGENETIC LINE OF THE APHID *Macrosiphum solanifolii* REARED CHIEFLY FROM APTEROUS PARENTS

With certain irregularities the features mentioned in Table IV are recognizable here also. See Experiment 270.

Genera-tion	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Vivipa-rous Females	Alate Vivipa-rous Females	Ovipa-rous (Sexual) Females	Males
I.....	Apterous	First	May 28-June 3	12	31	0	0
		Second	June 5-June 8	8	0	0	0
II.....	Apterous	First	June 12-June 16	31	25	0	0
		Second	June 18-June 25	3	5	0	0
III...	Apterous	First	June 27-June 30	49	64	0	0
		Second	July 2	35	73	0	0
		Third	July 4-July 5	33	48	0	0
IV....	Apterous	First	July 7-July 9	22	118	0	0
		Second	July 11	44	88	0	0
		Third	July 13	21	62	0	0
		Fourth	July 14-July 16	27	28	0	0
V.....	Apterous	First	July 18-July 21	47	29	0	0
		Second	July 23	7	7	0	0
VI....	Apterous	First	Aug. 17	7	0	0	0
		Second	Sept. 1-Sept. 9	27	0	0	0
VII..	Apterous	First	Sept. 11-Sept. 17	4	0	0	4
		Second	Sept. 19-Oct. 5	1	0	0	10
		Third	Sept. 21-Sept. 23	0	50	2	0
VIII .	Apterous	First	Sept. 25-Sept. 27	0	15	5	15
		Second	Sept. 29-Oct. 3	0	0	0	34
		Third	Oct. 5-Oct. 16	0	0	0	29
		Fourth	Oct. 11-Oct. 16	0	0	76	0
IX...	Alate	First	Oct. 18-Oct. 25	0	0	4	0

safe in assuming that these were of the same line. From one of them the sixth (?) and succeeding generations of Table VI were obtained.

Attention is directed in Tables IV, V, and VI to the following points:

1. The wingless viviparous females, more abundant early in the cycle, are gradually replaced by winged females. This is especially clear in Tables IV and V. It is obscured in Table VI by the fact that this line is not really a continuous one. A catastrophe in the fifth generation made it necessary to resume this line by means of a female from the same stock. Up to the fifth generation there is an irregular increase in the proportion of winged females, which reaches its climax in the fourth

generation. It is impossible to state what the fifth generation would have included, since only one fifth of the probable progeny were produced or survived. After the fifth generation up to the complete disappearance of viviparous forms, there was again a replacement—this time rather sudden than gradual—of the wingless females by winged ones. The same gradual disappearance of wingless viviparous in favor of winged females was observed in several other experiments of shorter duration which are not included in this paper, and has also been found in *Microsiphum destructor* by Miss Gregory (1917). It is therefore to be regarded as of general occurrence.

2. There is observed in two of the tables (IV and VI) a gradual increase in the tendency of wingless females to produce sexual females instead of males, as they most often do when the sexual phase begins. Thus in Table IV, generation IV, 2.5 per cent. of the sexual forms produced by apterous parents were sexual females. In generation V, 12.9 per cent. of the sexual forms were females. In the sixth generation, of the sexual offspring of apterous parents, 29.7 per cent. were females. In the seventh generation, which is the last from apterous parents, 73.3 per cent. of the sexual offspring were females. Thus, while the apterous parents produced mostly males during the sexual phase, there is a gradually increasing tendency to produce females. In Table VI is a brief indication of this same phenomenon. Males alone (of the sexual individuals) appear in the seventh generation, but a small number of females in the eighth generation. Unfortunately no apterous parents were available for a further generation. If it were possible to obtain wingless females in later generations it would be interesting to note whether they would not eventually produce only females.

Whether there is a similar progressive change in the sexual offspring of winged females is not so clear, since in none of the last three tables of this paper are there any male offspring of alate parents. However, in the

lower half of Table III there is an example of this kind. In the first generation from alate parents there is a minority of males; in the second generation no males. It is not improbable that, if a long line had been bred from alate parents, there would be a progressive decrease in the proportion of male offspring in the sexual phase of the cycle.

3. Tables IV, V, and VI also contain confirmation of the conclusion drawn from the earlier tables, namely, that at any given time winged viviparous parents produce more wingless viviparous offspring than do wingless parents, and that in the sexual phase males are produced chiefly by the wingless parents, sexual females by winged parents.

DISCUSSION

Although the most striking results of the foregoing experiments may appear to be the fact that winged viviparous females produce mostly wingless females in the parthenogenetic part of the cycle and sexual females in the sexual part, whereas the wingless viviparous females produce chiefly winged females in the parthenogenetic phase and males in the sexual, nevertheless the clue to the explanation of this phenomenon is more nearly discoverable in the progressive change in the frequency with which all forms occur in successive generations. Thus, there is a transition from a preponderance of apterous females early in the cycle to a predominance of winged females later. There is likewise, in the sexual portion of the cycle, a transition from males to sexual females. This latter transition has been demonstrated in the offspring of wingless mothers, and is indicated as probable in the offspring of winged females.

These transitions imply a gradual change of some sort, presumably in the metabolism of the animals. While the difference between a male and a sexual female, or between an apterous and an alate viviparous female, may be a definite morphological difference such as a difference in chromosomes, so that an individual is either the one or

the other, not an intermediate, it is hardly possible to escape the conclusion that the thing which brings about or prevents the morphological alteration is a gradual process. What this gradual change may be in the present case can not be known from the evidence, for obviously changes in the type of metabolism may be of various kinds.

Riddle (1917) conceives of such a change of metabolism as a change from individuals having a high rate of metabolism and low energy content to individuals having a low rate of metabolism and high energy content. In the eggs of pigeons forced to lay eggs continuously, he finds just such a change. The early eggs are of the former type, the late eggs of the latter type. From the early eggs are developed males, from the late ones females; and on those facts, supported by other work, Riddle bases an elaboration of the Geddes and Thompson theory of sex.

An attempt has been made to fit the facts obtained from aphids to Riddle's conception of sex. The gradual transition that occurs both in the parthenogenetic and in the sexual phase of the cycle of *Macrosiphum* indicates that one type of metabolism is prevalent early in the cycle, and the contrasted type late in the cycle. The fact that in this transition males precede sexual females shows that, if Riddle's hypothesis holds for the aphids, the progressive change is from a high rate of metabolism and low energy content to a low rate of metabolism and high energy content. Now it has been shown that wingless viviparous females precede winged ones, the change from the one form to the other taking place in part simultaneously with the transition from males to sexual females. Hence in accordance with Riddle's scheme wingless females should represent a high rate of metabolism and low energy content, while the winged ones should possess a low rate of metabolism and high energy content. With regard to the rate of metabolism alone, this assumption is supported by the fact that winged females require longer

to develop, that they produce fewer young per day, and that these young are on the average smaller than in the case of wingless females.

There are certain objections, however, to the foregoing conclusion. First, if winged viviparous females have a low metabolic rate while the wingless ones have a high rate, during the parthenogenetic portion of the cycle a parent with high rate of metabolism produces chiefly offspring with a low rate of metabolism, and *vice versa*; for wingless females produce chiefly winged ones, and winged females produce chiefly wingless ones. On the other hand, in the sexual part of the cycle, parent and offspring are both of the same metabolic type; for winged females (with low rate of metabolism) produce mostly sexual females (which in accordance with Riddle's view should possess a low rate of metabolism), whereas wingless females (high rate) produce mostly males (high rate). Why parent and offspring should be of a similar type of metabolism in the sexual phase, but of unlike type in the parthenogenetic phase, is not clear.

Unless the withholding of food increases the rate of metabolism, or unless the rate of metabolism is taken to mean not the absolute rate, but the rate relative to the food consumed, another objection to the assumption that the winged female possesses a lower rate of metabolism than the wingless ones is found in the work of Miss Gregory (1917). Miss Gregory finds that in *Microsiphum destructor* starvation of the apterous mothers results in the production of more winged offspring. It is only by assuming that starvation increases the rate of metabolism, or that "rate of metabolism" means the relative rate—rate relative to the amount of food consumed, not relative to the rate in another type of individual—that Miss Gregory's discoveries can be interpreted in support of Riddle's hypothesis; providing, of course, that the winged females have a lower metabolic rate than the wingless females.

If, to avoid either or both of the difficulties just men-

tioned, and notwithstanding the slower development, smaller young and smaller daily output of young of the alate females, these winged individuals be assumed to have a higher rate of metabolism than the wingless ones, other difficulties are encountered. This assumption would have the advantage of allowing parent and offspring to be of opposite metabolic type in both the parthenogenetic and sexual portions of the cycle, instead of being of opposite type in the parthenogenetic phase and of like type in the sexual phase. The transitions, however, would be in opposite directions in different parts of the cycle. In the parthenogenetic portion there would be a transition from a low rate of metabolism to a high rate (wingless to winged); while in the sexual part of the cycle the transition would be from high rate to low rate (male to sexual female). These opposite transitions would have to occur in part simultaneously, as in Table IV, fourth and fifth generations.

Unfortunately there has been no opportunity to determine experimentally the rate of metabolism in the various kinds of individuals in *Macrosiphum*; that is part of the program for the future. In the meantime, whether there is a fallacy in the foregoing argument, or a fallacy in Riddle's conception of the relation of metabolism to sex, can not be asserted with any degree of confidence.

Obviously the mere rate is not the only feature of metabolism that may conceivably be related to sex. If there are qualitative differences in the reactions that constitute metabolism, it seems to me more likely that these would influence the development of sexual organs than that the production of ovaries rather than testes could be determined by rate of metabolism alone. Qualitative differences in the reactions might entail differences in the rate of CO₂ production, and therefore be interpreted as quantitative differences. An increase in the output of lumber from a sawmill might be taken to indicate that the saws were running faster than formerly, whereas in reality the saws had been replaced by a new type of saw.

So long as rate of metabolism can be determined experimentally, while the precise reactions can not, there is every reason to continue the attempt to relate the rate of reaction to the course of development. But when facts come to light which do not easily fit preconceived ideas, it is highly important that alternate possibilities be kept in mind.

It is not impossible that the difficulties discussed above may be removed by discovering that the metabolic change that causes the transition from wingless to winged females is different from the change that causes the transition from males to sexual females. The two changes may be more or less independent of each other. In that case it may be possible to separate them experimentally. An agent may sometimes be found which will hasten or postpone the sexual reproduction without in any way affecting the transition from wingless to winged females in the parthenogenetic phase. If this agent hastened the sexual reproduction, it should act as a male-producing factor, since sexual forms would be introduced while wingless parthenogenetic females were more abundant. If, on the other hand, the agent delayed sexual reproduction, it should favor females, since the parthenogenetic mothers would then be more largely winged.

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